A phylogenetic analysis of behavioral neuro-ontogeny in precocial and nonprecocial mammals

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SUMMARY

Studies of the postnatal development of two groups of mammals are discussed in relation to behavioral change correlated with neurophysiological and anatomical data. The precocial mammals include especially the ruminants (sheep, cow; also horse and guineapig) while the nonprecocial mammals, which require a long period of nursing, include man and the primates, carnivores and rodents. Common features of certain neurological aspects of development are closely compared in this latter group to emphasize the importance of selected age studies to give correlative data from a wide variety of altricious species. For example, the relative age of a 1-2 week old mouse is equivalent to a 3-4 week old dog or 3 months in man in some behavioral features. The postnatal development of these several species is closely paralleled, but common features of the mother-offspring relationship, especially in dog and man, are not seen in the precocial mammals which are physiologically more independent at birth. These observations indicate that in the field of comparative medicine there is much to contribute by interpolating and extrapolating correlative data from different species. Some of this data in the neurologic field has been brought together in this paper, for especially in developmental and pediatric studies it is desirable to have cross-species data on relative postnatal ages in relation to the degree of maturity of the organism.

The duration of gestation is an unreliable index of the degree of neuromotor and behavioral maturation at birth, for additional factors, influenced by the postnatal environment, are involved. Precocial mammals, notably the horse (gestation 11 months), cow (gestation 9 months) and sheep (gestation 5 months) have relatively long gestation periods compared to the Carnivora, where the dog and cat have gestation periods between 8-9 weeks. Similarly rodents have a very short gestation period (mouse 18 days, rat 21 days). In those mammals having a short gestation period, their offspring are dependent on the mother for a long postnatal period. The primates and man also belong to this latter category of atricious animals, although, conversely, their gestation period is much longer (9 months). Precocious offspring of the former group appear to have less maternal dependency, for they are homeothermic at birth and show advanced neuromotor development and coordination. Behavioral mechanisms in this group, notably sheep, are such that the period immediately after birth is critical for the formation of primary social relationship (or establishment of a mother-offspring bond) (1) resembling imprinting in birds (2).

In nonprecocial mammals, however, there is a delay in the onset of the critical period of socialization during the neonatal period which is in part restrained by the immaturity of the animal. The onset of this period is like a slow awakening of the organism, and is a gradual process which is preceded closely by sensory and motor neural maturation. This period has been described in the mouse (3) and in man (4). The development of the dog and human infant has been compared (5) and the development of certain sensory and motor reflexes studied throughout the postnatal period in the dog (6, 7 and 8) and in the mouse (9).

Behavioral and physiological differences therefore exist between the two groups of newly born, the precocial and the nonprecocial, and this study involves comparative analysis of development of these two groups, and among different species of the nonprecocial group. From the evolutionary aspect, those mammals that are nest builders or lair dwellers (rodents and carnivores) or can give some form of contactual shelter protection (primates) have a shorter gestation, while those mammals that cannot give these forms of protection to their offspring must have mature offspring at birth capable of adultlike sensory-motor capacities. Maturity at birth by prolongation of the prenatal period in utero is therefore of survival value in such animals, affording some degree of protection against both en-

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vironment and predators (e.g. pigs, ruminants and cavies).

Precocial mammals. The ruminants make up the majority in this group. We have already referred to the behavioral features of this group, in that sensory and motor maturation at birth allows immediate identification with the dam to occur, and the establishment of a primary social relationship. Visual, auditory, olfactory and, to a lesser extent, gustatory, tactile and thermal stimuli can be appreciated by the newly born, and as righting reflexes, positive supporting and placing reactions are fully developed, together with almost adultlike postural abilities and coordination, the animal is able to associate independently with its environment, and is therefore relatively less dependent on its mother for protection. Survival in this group of animals is aided by the motor and sensory maturity of the offspring at birth.

Neurologic examination of a lamb immediately after birth reveals that sensory mechanisms are well developed, the sucking reflex is strong, and visual and auditory orientation responses and the startle reflex are present. After the initial hypotonia that is frequently seen immediately after parturition, muscle strength increases rapidly, and there is equal distribution of tone in the extensor and flexor muscles (or equality of reciprocal tonus) although there is generally weakness and incoordination until some hours after birth. Placing and supporting reactions are strong, but the hopping reaction is weak until some hours after birth. Labyrinthine righting responses crudely influencing limb and body positions cause head oscillations (spasmus nutans, due to overactive righting responses) and neck swinging which are corrected by a wide-base stance in the forelimbs. This phase passes rapidly as adultlike attitudinal and postural responses develop. The ability of this group of animals to stand upright at birth may suggest that the proprioceptive mechanisms involved in maintaining a positive supporting reaction do so by causing hypertonia of the extensor muscles, converting the legs into supporting "pillars" (i.e. pillar-supporting reaction). With the offspring suspended so that the feet are not allowed to contact the ground, passive manipulation of the limbs reveals that extensor tonus is slightly greater than the flexor, while the contact placing response tends to be hyperactive, in that the limb, on making contact with the ground, is extended maximally. By three days of age in the lamb, this reaction is less pronounced and movements of limbs are more refined, and composite postural and attitudinal reactions are more perfectly controlled.

Nonprecocial mammals. This group consists of a phylogenetically extreme collection of mammals, ranging from the rodents, through the carnivores, to the primates and man. In all these species, the immediate postnatal period is characterized by great maternal dependency, and a long delay in the onset of primary social relationships due to immaturity of sensory and motor abilities. Some olfactory, gustatory, thermal and tactile conditioning or learning does occur, warmth and nutriment being the main stimuli in the mother-offspring relationship. Also, as the offspring are poikilothermic (e.g. in the dog and mouse) and unable to control their body temperature until several days after birth, the maternal (or nest) environment controls this, and protects the animal from the external environment. Thermal and tactile stimuli are important in maintaining the mother-dam relationship, as are visual and auditory cues from the offspring to the dam (10 and 11).

Only when physiological mechanisms change and become more adultlike (changes in ingestive and excretory behavior patterns, adultlike locomotor and sensory abilities allowing exploration of the external environment), especially at the time of weaning, does the offspring begin to asssociate stimuli, develop conditioned (and emotional) reactions, and enter the critical period of socialization. In man, carnivores and rodents, this sequence of behavioral maturation is markedly similar, although traumatic experiences during the neonatal period, and more especially during the critical period of socialization can have great influences on the later behavior of the animal (4 and 12). Also neurologic development among these different species is essentially similar, and an account of some of the more important reflexes will be presented and compared. It is accepted that behavioral changes during development are indicative of neurologic maturation, but as the interpretation of the expression of behavior by the subject is more difficult to compare among subjects of different species, reflexes, which are specific and stereo-

Table 1 — Approximate age when response changes (disappears or adultlike)

Reflex	Man (17, 19)	Dog (8)	Mouse (9)
Rooting	11-12 m.	13 d.	9 d.
Hyperkinesias (coarse tremors)	2 m.	21 d.	10 d.
Auditory startle	Present at birth	25 d.	12-14 d.
Visual orientation (following response)	Present at birth	26 d.	—
Magnus (tonic neck and labyrinthine)	3-6 m.	17 d.	6-8 d.
Mass movements (generalized responses, e. g. to pain)	3 m.	21 d.	9 d.
Postural flexion (in vertical suspension)	3-4 m.	3 d.	6 d.
Postural extension (-do-)	4-6 m.	19 d.	10 d.
Righting (otolith)	2-3 m.	present 1 d.	present 1-2 d.
Crossed extensor	3-4 m.	15 d.	4 d.
Mature relaxed phase	—	26 d.	12-14 d.
Primitive stepping	7 m.	1 day	1 day
Forelimb placing (visual)	5-6 m.	27 d.	12-14 d.
Forelimb contactual placing	—	6 d.	1 day
Eyes open	at birth	10-13 d.	11-12 d.
Subcortical and spinal responses weaken (cortical dominance)	3 m.	19-21 d.	8-10 days
Reciprocal kick reaction	4 m.	15 d.	5 d.
Voluntary elimination	appears 22-24 m.	appears 23 d.	appears 12-14 d.
Emotional reactions	appears 6-12 m.	appears 21 d.	appears 12 d.
Visual fixation	appears 4 m.	28 d.	—
Auditory orientation	appears 4 m.	27 d.	16 d.

typed and not subjected to the same variables, can be compared and contrasted more precisely (see Tables 1 and 2).

Innate reflex responses in the dog (8), human (13), and mouse (9) notably the rooting, head orientation and labial sucking reflexes in all three species, and positive thigmotaxis, positive thermotaxis and negative geotaxis in the dog and mouse can be elicited at birth and may be regarded as innate behavioral mechanisms that ensure the newly born can find warmth and shelter, locate the nipple and feed. There is a change in the nature of these superficial sensory reflexes during the neonatal period; they are more easily elicited and it would appear that some conditioning of these innate responses, indicative of early learning, has occurred. Towards the end of the neonatal period these responses disappear as more complex mechanisms take over, associated with greater sensory capacities, homeothermy and alterations in the mother-offspring relationship at weaning with concurrent changes in ingestive and excretory activities in the dog (8) and mouse (3). It must be remembered that these two species are blind, deaf and poikilothermic at birth, and the main afferent stimuli that can be appreciated, and which reflexively evoke behavioral responses, are thermal, tactile and gravitational responses. Studies of myelination in the dog and human infant show that the degree of myelination is proportional to the functional capacities of the organism at a certain age; optic and auditory nerves are poorly myelinated in the newborn dog, for example, but those nerves concerned with body righting and negative geotropism (nonacoustic portion of 8th cranial nerve), head orientation and teat location (5th cranial nerve) and sucking ability (7th cranial nerve), are well myelinated in the neonate (5). The development of reflexes and behavior in relation to brain maturation in the cat, rat and guinea pig have been studied (14), and the sequential development of myelin-

Table 2

	Myelination of major tracts	Cellular maturation	EEG	Sensory-motor maturation	Conditionability	
					Unstable	Stable
Mouse	14 days	14 days	13-15 days	14 days	—	—
Dog	After 4 weeks	28-32 days	28 days	25-28 days	14 days	21 days
Man	24m.	24 m.	24 m.	24 m.	birth	6 weeks

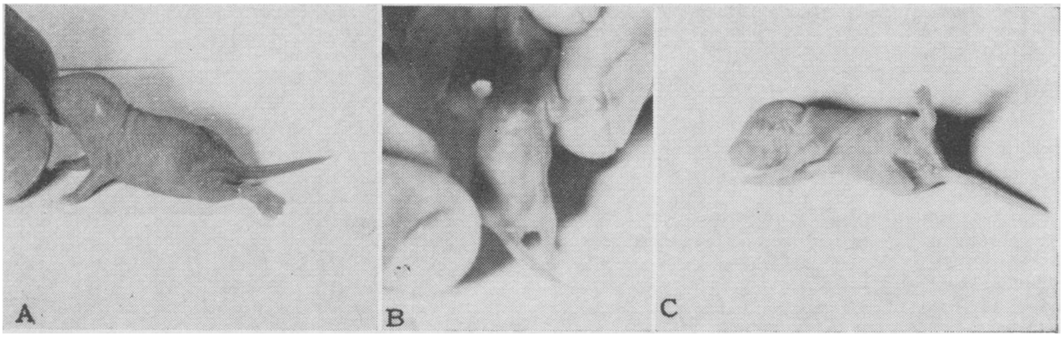

Fig. 1. Some responses of the newborn mouse seen also in dog and man — a—Rooting reflex. b—Crossed extensor reflex. c—Righting reflex.

ization of the brain of the rat examined and compared with other species such as the opossum, cat and guinea pig (15).

Behavioral studies have divided development into neonatal, transitional, socialization and juvenile periods of development, and, even though development is a gradual and sequential process, these periods can be clearly differentiated by both behavioral observations and neurologic tests. From the tables we see that specific changes occur at approximately 3 months, 3-4 weeks and 1-2 weeks in man, dog and mouse respecttively, where subcortical and spinal responses disappear as cortical development causes progressive inhibition of these primitive responses; this is the end of the neonatal period, and the transitional period follows. The period of socialization, or time when sensory capacities and locomotor abilities are more adultlike, commences at approximately 4 weeks in the dog and two

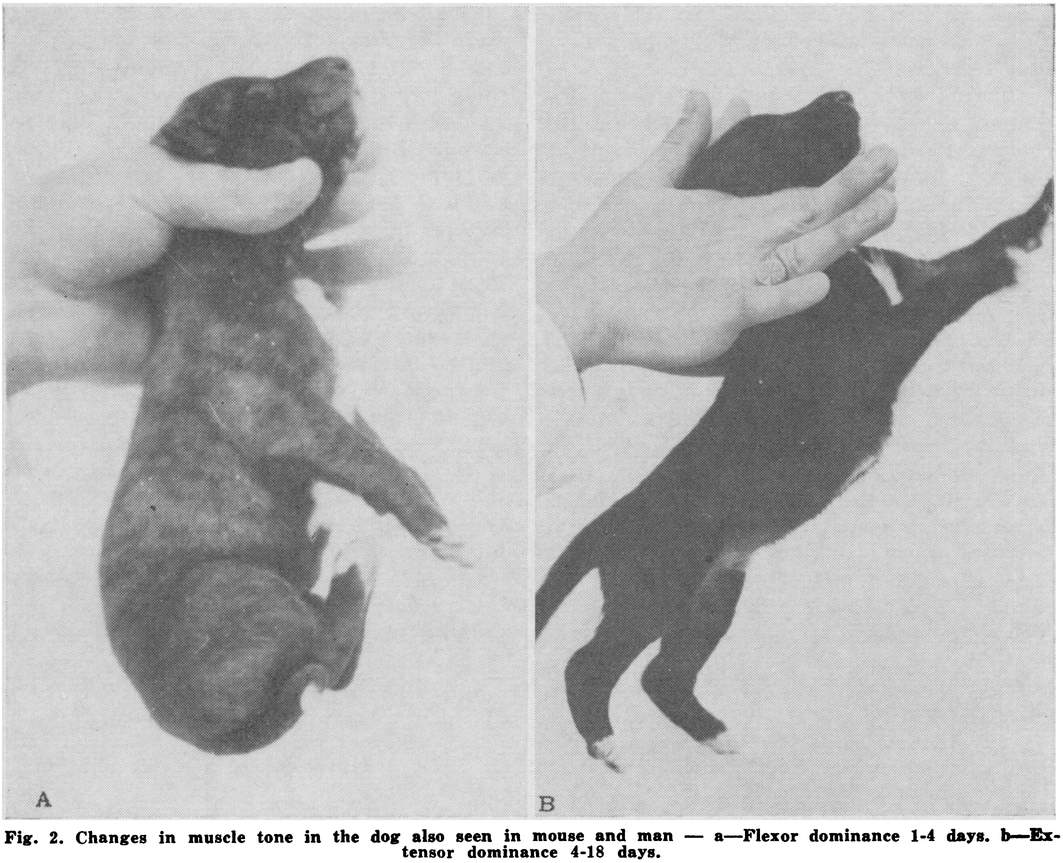

Fig. 2. Changes in muscle tone in the dog also seen in mouse and man — a—Flexor dominance 1-4 days. b—Extensor dominance 4-18 days.

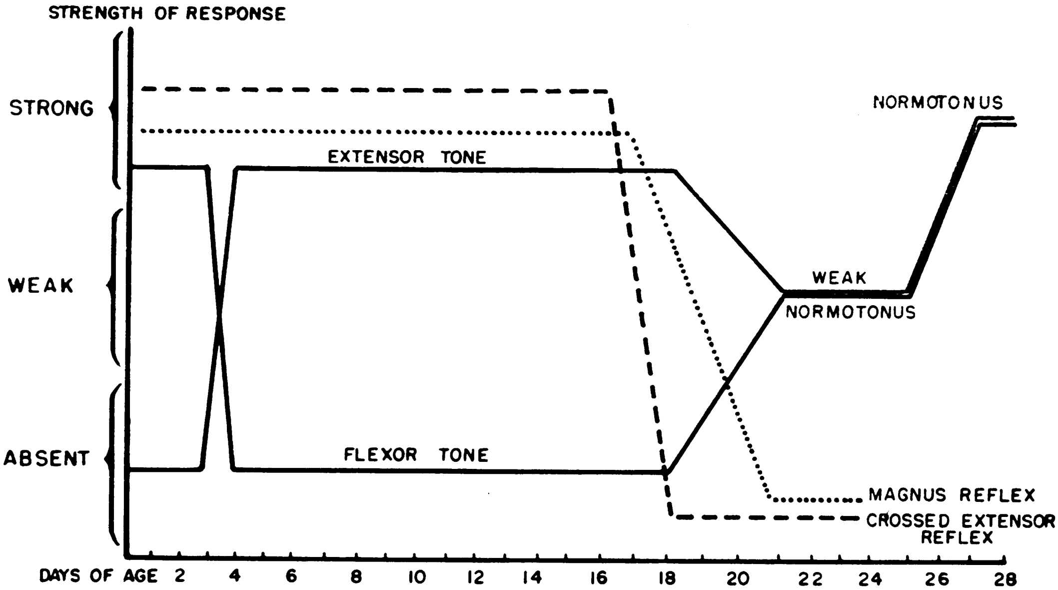

Fig. 3. Neuro-ontogeny of motor responses in the dog.

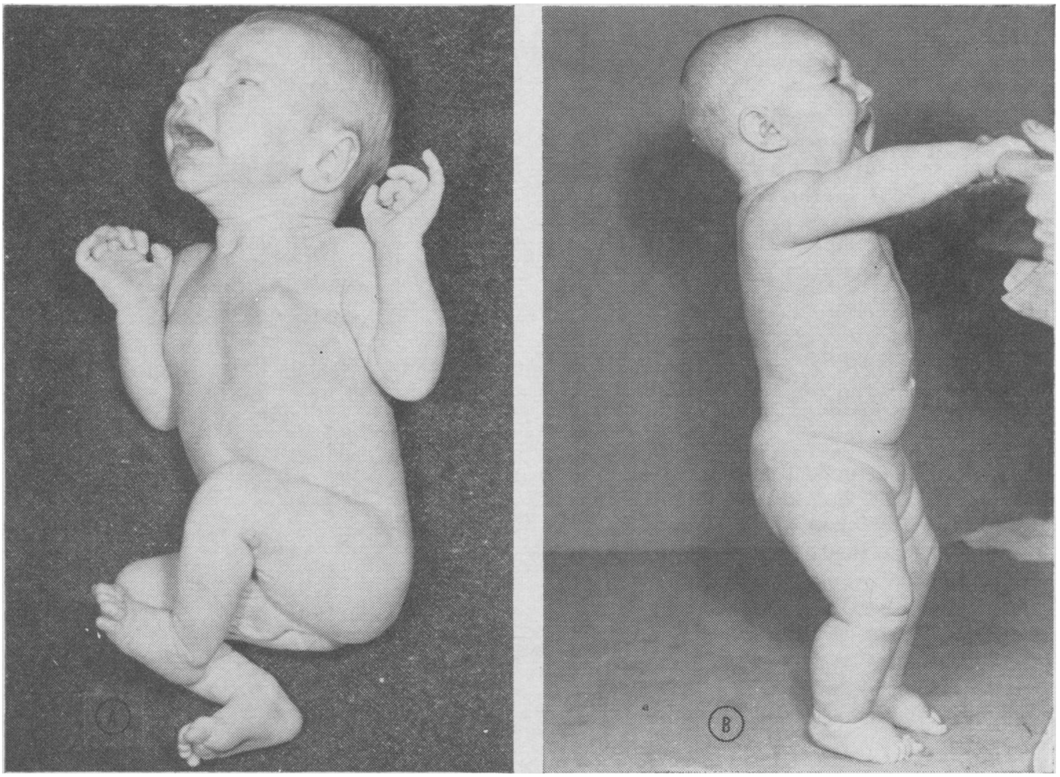

Fig. 4. Flexor (a) and extensor periods (b) in new born and 4 month old infants. (courtesy Dr. T. T. S. Ingram).

weeks in the mouse, while in man, sensory and motor maturation is less rapid, extending over a period between 6-12 months. Early symmetry of limb positions and residual fetal responses are seen in the neonate of all three of these species, and a gradual cephalocaudal acquisition of motor skill (placing and supporting reactions in man, dog and mouse, and grasp reflex and Babinski in man and mouse) with the dampening and gradual inhibition of primitive responses is seen. Developmental correlates of myelination, reflexes, EEG and behavior in the mouse (16), dog (8) and man (17) illustrate these phenomena are common to all these forms of altricious mammals, although the locomotor abilities of the newborn dog and mouse are superior (primitive crawling and pivoting) in spite of poorly developed control of the hind limbs (Figs. 1-3). The decreasing effect of postural changes on muscle tonus as higher nervous centers develop by using spinal and decorticate animals has been shown (18).

The elicitation of these reflexes characteristic of the various levels of neurologic maturity constitutes a regime of developmental neurologic diagnosis (13 and 19).

Muscle tone tends to be continuous, but is altered slightly by postural changes, and the distribution of muscle tone also alters with age as higher centers of nervous activity develop. Almost identical changes in muscle tone in the human (see Figs. 2 and 3) have been described (20).

Discussion and conclusion

A cross sectional study of neurologic or behavioral development or of pathophysiologic problems such as anoxia or immune responses of the newly born, or psychological studies of the ontogenesis of learning and conditionability in different mammals is of greater anthropomorphic value if the experimental animals used are of the same category as the human neonate. Comparisons of phylogenetically different species having similar postnatal periods of development and physiological immaturity may be more assuredly made than in studies where more precocious newly born are used. By constructing a chronological series of developmental processes (3, 14, 19), what must be studied in utero in one species may be adequately investigated in the newly born of another. The time at which a certain experimental procedure is commenced is also critical, for the effect on the newly born of one species may have the same effect as on a much older animal of a different species. Also, the development of both enzymatic and behavioral systems may be difficult to study in one particular species, which only gives an indication as to the particular phenomenon involved. The process of socialization and imprinting in sheep, for example, is extremely rapid within the first 24 hours of life, while in the dog and human similar phenomenon develop more gradually and so may be investigated more thoroughly and precisely at a later age.

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